Subsurface Aquatic Ecology of Mammoth Cave

14

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Abstract

The hidden nature of Mammoth Cave National Park's (MCNP) cave aquatic ecosystem may suggest it is disconnected from events occurring on the surface. However, it is part of a continuum of water that begins with rain falling within the Green River watershed upstream of Mammoth Cave. Locally, water drains through Mammoth Cave's 184 km^2 (71 square mile) watershed and ends with the master stream for south-central Kentucky, the Green River. Rain falling in an area underlain by insoluble rock, such as sandstone on the Chester Upland, flows overland as runoff until it reaches a crevice, where it feeds a sinking stream or vertical shaft below. Rain falling on an area underlain by epikarst, the layer of highly weathered limestone and soil just beneath the surface common in the Mammoth Cave region, either percolates relatively slowly through interconnected vertical and horizontal channels (Fig. 14.1) or flows rapidly through a sinkhole. Whether water moves slowly or rapidly through this unsaturated zone of partially water-filled channels it ultimately reaches the water table and flows out of springs along the Green River (Fig. 14.2). When the Green River rises during floods, springs and base-level cave streams temporarily reverse their flow. A combination of back-flooding and local water influx can cause water levels in the cave to rise as much as 18 m (60 feet). During water's journey through the cave aquatic ecosystem, it transports organic matter, and often contaminants, from the surface. This is a greatly simplified description of the Mammoth Cave region's hydrogeology and vulnerability to pollution (see Chaps. 6, 8 and 18 for more information), but it is important for understanding the interplay between the nonliving components of the cave aquatic ecosystem, the organisms living there, the structure of their communities, and the impact of human activities.

> *It takes generosity to discover the whole through others. If you realize you are only a violin, you can open yourself up to the world by playing your role in the concert.*
>
> —Jacques Yves Cousteau

14.1 Habitat Types and Organisms

Absent the effects of human activities on surface water quality, the reliability of water is one of the major limiting factors for cave aquatic communities in upper level habitats in the Mammoth Cave area (Poulson 1992) and generally increases from the unsaturated zone to the water table (Fig. 14.3).

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Fig. 14.1 Icicles flowing from underground channels at a roadcut in MCNP demonstrate the vertical and horizontal flow of water through the epikarst. *Photograph* by Kurt Lewis Helf

14.1.1 Epikarst

Located at the top of the unsaturated zone, the epikarst is an ecotone, or transitional habitat, between surface and cave ecosystems. As such, ecotones exhibit a blend of environmental conditions and organisms from these very different ecosystems. Forest and grasslands on the surface supply the epikarst with tiny particles and molecules of organic matter, but the perpetual darkness in epikarst is a feature of subterranean habitats. Epikarst is a permanent habitat for many small surface and cave aquatic organisms (Pipan et al. 2006; Pipan and Culver 2013).

Epikarst drainage into the cave also creates a wide variety of isolated, diverse temporary habitats such as thin films of water on cave speleothems, drip pools (Fig. 14.4), and seeps at collapsed areas (Barr and Kuehne 1971). Aquatic organisms found in these habitats may include those from the surface such as cladocera, copepods, earthworms, fungi, nematodes, ostracods, and protozoa (Culver and Pipan 2009; Pipan et al. 2006). These temporary habitats also harbor a number of stygobionts, organisms only found in cave aquatic habitats, including the eyeless, unpigmented isopod *Caecidotea stygia*, the amphipod *Crangonyx barri*, which can be eyeless and unpigmented or not, the eyeless, unpigmented amphipod *Stygobromus vitreus*, the aquatic earthworms *Aeolosoma* and *Chaetogaster*, and the unpigmented flatworms *Sphalloplana percoeca* or *Sphalloplana buchanani* (Hubricht 1943; Gittleson and Hoover 1970; Barr and Kuehne 1971; Kenk 1977; Lewis 1988; Zhang and Holsinger 2003; Culver et al. 2010). Some permanent residents of the epikarst are unlikely to survive long-term if they are deposited in temporary cave pools. Hypothesized sources of mortality for epikarst organisms in drip pools include predation, lack of suitable habitat, reduced/absent reproduction, and competition for relatively scarce dissolved organic carbon (Pipan et al. 2010). The organic carbon in drip pools supports a thin film of bacterial colonies coating the substrate which largely feeds grazers such as flatworms (Simon et al. 2003). Water levels in these temporary habitats will decrease considerably and often dry out completely during droughts. However, rains that follow eventually replenish pools with water, organic matter, and organisms from the epikarst.

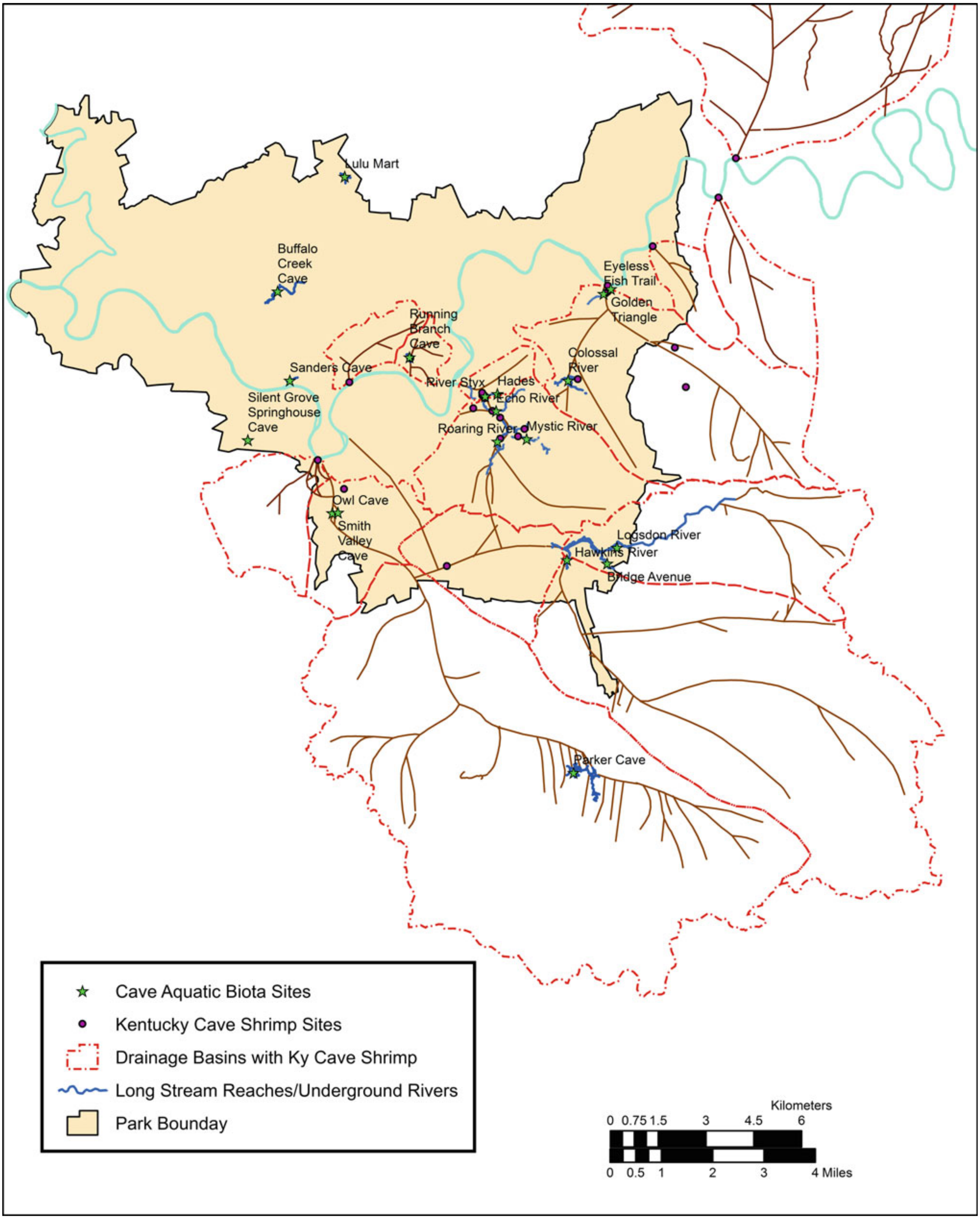

Fig. 14.2 Major karst groundwatersheds/basins of Mammoth Cave National Park, springs, and locations of surveyed cave aquatic communities in human accessible cave streams/rivers. Note the difference among basins in the proportion of land outside MACA boundaries. Map courtesy of Rickard Toomey

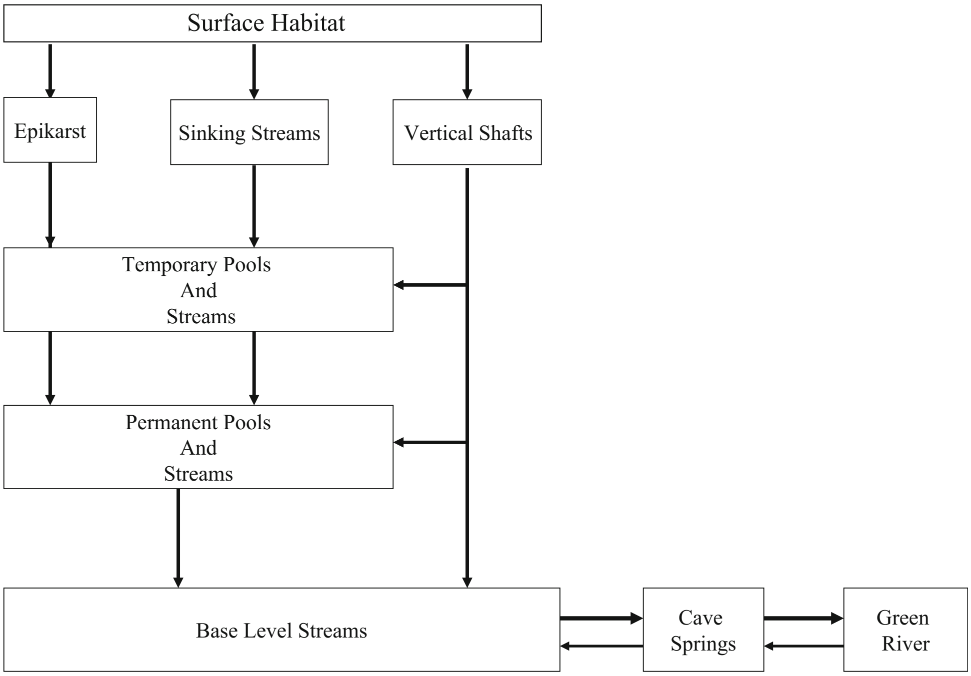

Fig. 14.3 Conceptual model of water's journey from the surface to the Green River in the MCNP region

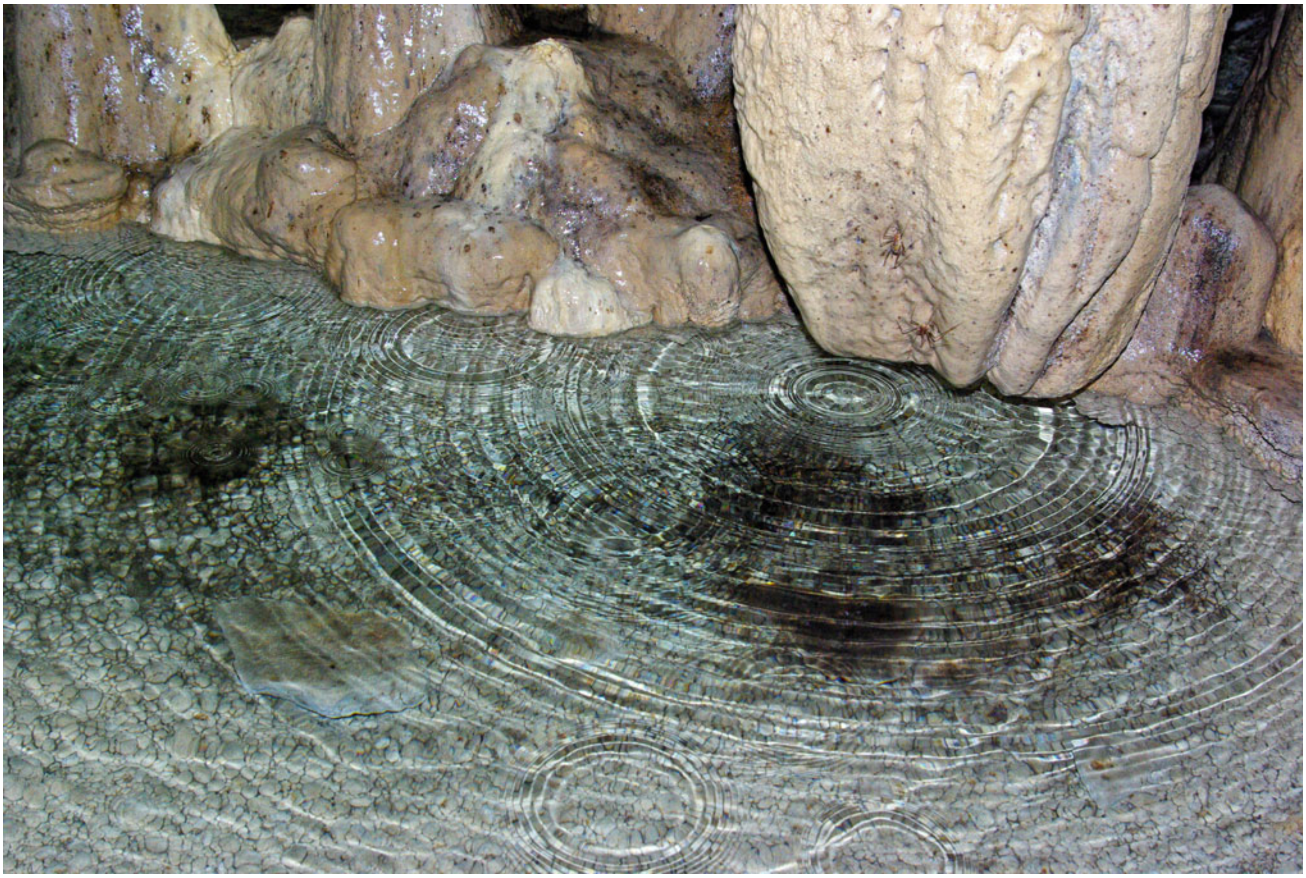

Fig. 14.4 Epikarst drip is the source of water for this pool in White Cave. *Photograph* by Kurt Lewis Helf

14.1.2 Shafts

Water flowing off the sandstone caprock onto the limestone sinks and may form shafts where water can plummet directly to mid or lower levels (Fig. 14.5). Being storm driven, these sources of water flowing into the cave are more variable than epikarst flow. The community of aquatic organisms found in streams and pools fed by shaft drains is transitional in that stygobionts become more prevalent than epikarst organisms. The small eyeless, unpigmented amphipod *Stygobromus exilis* (Fig. 14.6), is a generalist widely distributed among cave aquatic habitats and replaces the epikarst specialist *S. vitreus* (Lewis 1988; Culver et al. 2010). Another amphipod associated with cave streams, *C. barri*, may also be found. The isopod *C. stygia* typically inhabits upper level shaft drain streams, whereas in lower levels both *Caecidotea bicrenata* and *C. stygia* may be occasionally be found together in disturbed areas (J.J. Lewis personal communication). The blind, unpigmented cave crayfish *Orconectes pellucidus* are occasionally found in isolated pools. These crayfish are known to be scavengers but are also predators (Hobbs III and Daniel 1977).

Fig. 14.5 Water flow into the Maelstrom; an example of a vertical shaft. *Photograph* by Rickard A. Olson

Fig. 14.6 Epikarst specialist amphipod (*Stygobromus vitreus*). *Photograph* by Rickard A. Olson

14.1.3 High-Gradient Streams Above Base Level

Water from shaft drains and overflowing drip pools collect to form permanent flowing streams. Examples in Mammoth Cave include much of Mystic River, all of Logsdon River (Figs. 14.2 and 14.7), Eyeless Fish Trail, and River Acheron. Stygobionts found in these high-gradient streams are more adapted to food poor conditions compared with their closest surface relatives. Stygobionts display enhanced sensory organs, which enable them to find scarce or low-quality sources of food more easily. For example, the Southern cave fish *Typhlichthys subterraneus*, a blind, unpigmented species found in these high-gradient streams, possesses higher numbers of sensory organs and corresponding expansions in its brain, than its closest surface relative the cave springfish *Forbesichthys agassizii* (Niemiller and Poulson 2010). The Southern cave fish is highly sensitive to distant vibrations in the water and can more easily locate the patchily distributed copepods, isopods, amphipods, small crayfish, and salamander larvae or even smaller cave fish on which it feeds. These streams may also support large numbers of cave crayfish *O. pellucidus*. The highest density was 376 individuals per 5000 m^2 in a section of Logsdon River (Pearson and Jones 1998). These crayfish are wide ranging foragers and can even move overland between isolated pools as long their gills do not dry out (Fig. 14.8).

In nutrient-enriched cave streams, the surface crayfish *Cambarus tenebrosus* can be highly abundant and may even be able to reproduce and, in this context, likely out-competes *O. pellucidus* since it is larger and stouter-bodied. However, in the most recent surveys of Park cave streams, densities of these crayfish never rose above 29 per 5000 m^2 (Pearson and Jones 1998). Thus, in cave streams with low food availability, the cave crayfish's significantly longer antennae enable them to locate food more efficiently than the surface crayfish (Ziemba et al. 2003; Taylor et al. 2010). Other cave invertebrates commonly found in these high-gradient streams include the isopod *C.*

Fig. 14.7 Logsdon River, an example of a high-gradient cave stream above base-level, flows into P. Strange Falls. *Photograph* by Gary Berdeaux

bicrenata (occasionally, with *C. stygia*), the amphipod *S. exilis*, and *Sphalloplana* sp. flatworms.

14.1.4 Base Level

Ultimately, all water moving through these habitats reaches the water table, or base level, which is equivalent to the elevation of the Green River near that part of the cave (Fig. 14.9). One of the more highly adapted cave fishes is the blind, unpigmented Northern cave fish *Amblyopsis spelaea*. It is a top predator that reaches its highest abundance in Roaring River, an excellent example of a base-level stream in the park (Figs. 14.2 and 14.10). Another highly adapted organism observed at base level is the unpigmented, eyeless Kentucky cave shrimp *Palaemonias ganteri*, a federally listed endangered species (Fig. 14.11). Its highest estimated density to date (i.e., 1308/5000 m^2) was documented during a survey of Mystic River, a tributary of Roaring River on the south side of the Green River, only slightly above base level (Pearson and Jones 1998). Since *P. ganteri* is found in cave streams on both sides of the Green River (Table 14.1), a potential geographic barrier to genetic exchange between populations, it is possible there is more than one species. These shrimp are thought to feed on the microorganisms living in the sediment, which it has been observed filtering

Fig. 14.8 Cave Crayfish (*Orconectes pellucidus*) can walk overland between cave pools and streams. *Photograph* by Kurt Lewis Helf

through its mouthparts (Cooper and Cooper 2010). Roaring River is also the habitat of the eyeless, unpigmented shaggy cave snail *Antroselates spiralis*. Other cave aquatic biota found in base-level streams include the isopod *C. bicrenata*, the amphipod *S. exilis*, *Sphalloplana* sp. flatworms, the cave crayfish *O. pellucidus*, the Southern cave fish *T. subterraneus*, occasionally, the cave spring fish *F. agassizi,* and the sculpin *Cottus carolinae*.

The diversity of aquatic organisms in base-level streams, particularly those associated with spring outlets, is partially attributable to aquatic invertebrates from the surface. Whitman (1989) samplers in base-level cave sediments and Barr and Kuehne's (1971) plankton collections from base-level streams found myriad surface aquatic organisms such as diatoms, filamentous green and blue algae, flatworms, and roundworms. Barr (1967) collected surface rotifers in park cave streams, whereas Whitman (1989) speculated some rotifer species he found might have been cave adapted and new to science. Oligochaetes, or segmented worms, such as *Aelosoma*, *Chaetogaster*, tubificids, and enchytraeids were reported by both Barr and Kuehne (1971) and Whitman (1989) in cave stream sediments. Whitman also found the larvae of at least five different genera of midges, occasionally in high densities, living in the sands of cave streams such as Echo River. While it is unknown whether adult midges can survive or reproduce in the cave, it is clear that at least their larval stages play some role in the park's cave aquatic ecosystem. Barr and Kuehne (1971) and Whitman (1989) regularly found cladocera and copepods in their zooplankton samples; and Barr and Kuehne (1971) observed both water fleas and copepods bearing young and egg sacs. They attributed winter increases in zooplankton to the influx of water and detritus from percolating ground water, sinking streams, and backflow from the Green River. They also speculated the increased zooplankton density they found in summer and fall were due to secondary microbial production in cave pools and streams, based on detritus carried in by floods.

Fig. 14.9 Roaring River; an example of a base-level cave stream. *Photograph* by Rickard A. Olson

Relatively recent biological monitoring in Roaring and Echo/Styx rivers (Pearson and Jones 1998) found aquatic vertebrates from the surface such as salamanders, frogs (*Rana palustris*, *R. clamitans*), toads (*Bufo woodhouse fowleri*), and surface fishes. There is no good evidence surface aquatic organisms make a significant contribution to the cave aquatic community as predators. However, two fish species, the Spring Cavefish (*F. agassizii*) and the Banded Sculpin (*C. carolinae*), are regularly observed, though in low densities, in base-level streams associated with springs in the park (Pearson and Jones 1998; Niemiller and Fitzpatrick 2012). *F. agassizii* may be found in both surface and cave streams which classifies them as stygoxenes (Culver and Pipan 2009; Niemiller and Fitzpatrick 2012). Gut contents indicate *F. agassizii* in cave aquatic habitats feeds on amphipods, midge larvae, and worms (Niemiller and Poulson 2010). Gut contents from *C. carolinae* in surface streams indicate they feed on aquatic insects, crayfish, isopods, amphipods, snails, and other fish (Poly and Boucher 1996; Tumlinson and Cline 2002).

14.2 Energy Input

Inputs of photosynthetically derived organic matter from surface ecosystems, such as dissolved organic matter leached from the vegetation litter–soil interface (think of water percolating through coffee grounds to produce coffee), appear to be the dominant source of energy input to the cave aquatic ecosystem in the Mammoth Cave region (Fig. 14.12). Indeed, temperature, precipitation, and forest biomass, indicators of primary productivity on the surface and the availability of organic carbon, were all found to be important factors in predicting the presence of cave organisms (Christman et al. 2016). Flow reversals and back-flooding from the Green River into cave springs also transport

Fig. 14.10 Northern Cave Fish (*Amblyopsis spelaea*). *Photograph* by Matt Niemiller

Fig. 14.11 Kentucky cave shrimp (*Palaemonias ganteri*). *Photograph* by Michael Durham

Table 14.1 Drainage basins, caves, and cave streams in which Kentucky cave shrimp (*Palaemonias ganteri*) have been found. Localities based on United States Fish and Wildlife Service (1988) and data in Mammoth Cave National Park files

Drainage basin	Cave/Spring	Site
McCoy Bluehole		
	McCoy Bluehole Spring	
Suds Spring		
	Suds Spring	
Mile 205.7		
	Mile 205.7 Spring	
Pike Spring		
	Northtown Cave	Lower level stream
	Roppel Cave	Grand Central Sump
	Colossal Cave	Colossal River
	Unknown Cave	Eyeless Fish Trail
	Unknown Cave	Golden Triangle
	Pike Spring	
River Styx		
	Mammoth Cave	Hades
	Mammoth Cave	River Styx
Echo River		
	Mammoth Cave	Echo River submerged passage
	Mammoth Cave	Echo River
	Mammoth Cave	Roaring River
	Mammoth Cave	Shrimp Pools
	Mammoth Cave	Mystic River
	Mammoth Cave	Lucy's Dome Drain
Running Branch		
	Running Branch	Reccius River
Ganter Bluehole		
	Ganter Cave	
Turnhole		
	Lee Cave	Snake River
	Whigpistle Cave	Red River
Turnhole—Double Sinks		
	Sandhouse Cave	Sandhouse Cave Spring

organisms and photosynthetically derived organic matter into the cave aquatic ecosystem.

14.2.1 Green River Flow Reversals and Back-Flooding into Cave Streams

Flow reversal events are a normal and vital part of cave aquatic ecosystem function in Mammoth Cave. When the Green River rises above nearby cave streams the river flows into, rather than out of, cave springs. This backflow will continue until surface and subsurface water levels equalize and normal flow out of cave springs resumes (see Chap. 8 for more information on this phenomenon). These flow reversals carry particulate organic matter and myriad surface aquatic organisms (e.g., surface fishes) that greatly contribute to food energy input. A recent study of surface fish captured in Mammoth Cave's base-level streams yielded 22 species from nine families over two field seasons (Ruhl 2005).

An unusual back-flooding relationship exists at times when Green River water enters River Styx Spring and exits Echo River Spring, a straight line mile (1.6 km) to the south. In a recent three-year study, water temperature was used as a proxy to determine the direction of flow (Trimboli et al. 2016). The authors reasoned that during flow reversal events, water temperatures in Styx and downstream Echo Rivers, typically above or below that of the Green River,

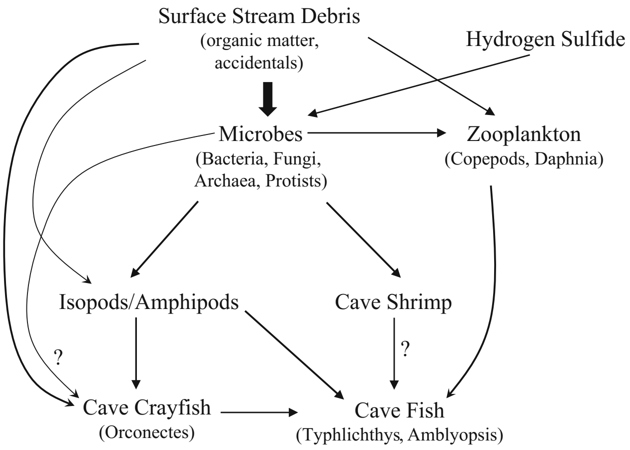

Fig. 14.12 Hypothesized food web diagram for cave aquatic habitats in MCNP region. *Arrows* indicate the direction of energy flow. Modified from Barr and Kuehne (1971)

would be similar to Green River water temperatures. Their data showed only River Styx underwent dramatic deviations from its mean temperature of 13.5 °C ± 2.5 reaching a maximum of 23.8 °C and a minimum of 3.6 °C (Trimboli et al. 2016). Water temperature in Echo River, upstream of the area affected by flow coming from River Styx, remained relatively stable at 13.4 °C ± 0.6. Over the three-year study, their temperature data showed that these flow reversal events occurred an average of five times each year.

14.2.2 Shifting Paradigm

The long-standing paradigm among cave ecologists was that the cave aquatic ecosystem was almost exclusively supported by particulate organic matter (POM: leaves, twigs, etc.) washed in from the surface. Logically, increased POM input should support more stygobionts. Yet data collected at Mammoth Cave over many years show no discernible relationship between POM and stygobiont density. For example, cave streams with low POM (Logsdon River/Bridge Avenue) had high stygobiont densities and cave streams with high POM (Mystic River) overall, with the exception of cave shrimp, had lower densities of stygobionts (Table 14.2). Cave streams have been generally thought to have low POM supply compared with surface streams. However, data from MCNP indicate there are a few exceptions to the general assumption of the old paradigm. For example, Pearson and Jones' (1998) POM data from nine cave stream reaches in Mammoth Cave ranged from 12.7% at Mystic River, remarkably nearly double Whitman's (1989) data from surface streams, to 1.4% at Echo/Styx (Table 14.2). However, POM from the surface is mostly processed by consumers (e.g., amphipods and isopods) near its point of entry into cave streams, and dissolved organic carbon is a more important source of carbon in deep cave habitat (Simon and Benfield 2001; Simon et al. 2007).

14.3 Food Web

Compson (2004) analyzed ratios of carbon and nitrogen isotopes in the tissue of biota from Mammoth Cave's surface streams, springs, and cave streams to evaluate their food sources and feeding relationships. Because carbon is relatively stable between trophic levels, differences in the ratios of carbon isotopes in animal tissue are used to determine an organism's food sources. Nitrogen, however, is enriched as it moves through successive trophic levels, and so increased ratios of nitrogen isotopes in an organism's tissues can differentiate between producers and consumers among the ecosystem's constituent organisms. He concluded periodic back-flooding events through cave springs likely contribute substantial pulses of nutrients to the cave stream community. Surface fish trapped in cave streams are a clear example of food input from the surface because after their inevitable death, they become food for stygobiont scavengers. Similarly, the surface crayfish *C. tenebrosus*, while not abundant in MCNP cave streams, is frequently encountered in cave streams and might subsist on detritus washed in from the surface. Compson's nitrogen isotope data place *C. tenebrosus* in a low trophic level and its carbon isotope data are close to that of detritus and fungal mycelia.

Compson's (2004) data on carbon and nitrogen isotopes offer some insight into the cave stream community's ultimate food source and its feeding relationships. Carbon isotope data clearly show the ultimate food source of MCNP's stygobionts is derived from bacteria (Fig. 14.13), likely as bacterial biofilms, and so provides support for the new paradigm. Carbon isotopes in stygobiont tissues were enriched relative to detritus, which suggests it is not the food source of their prey. Since the cave crayfish *O. pellucidus* is known to be at least partially predatory, it is not surprising its enriched nitrogen isotope levels place it in one of the upper trophic levels. Interestingly, the nitrogen isotope data for the cave isopod, presumably *Caecidotea* sp., place it near *O. pellucidus* trophic level suggesting that it, too, is partially predatory. Finally, enriched nitrogen isotope levels in the Southern cave fish (*T. subterraneus*) indicate that it, of the stygobionts tested, occupied the highest trophic level and so is one of two top predators in MCNP's cave stream communities. Presumably the Northern cave fish *A. spelaea*, though its tissue was not tested, occupies a similar position. These trophic relationships, however, are generalizations of what are likely much more complicated interrelationships within cave stream communities (Fig. 14.12). As yet, we have limited data regarding the origins of the dissolved organic matter that fuel the bacterial communities driving the

Table 14.2 Density of stygobiotic and Stygophilic fauna in Mammoth Cave area subsurface streams as a function of their length, coarse particulate organic matter, and microbial biomass

Reach	Basin	Reach length (m)	Coarse particulate organic matter (% weight LOI)	Microbial biomass (m mol/g)[d]	Mean density of stygobiotic fauna/5000 m^2	Mean density of Stygophilic fauna/5000 m^2
Echo and Styx Rivers	Echo Spring and River Styx	835	1.3–2.1[a]/1.4[c]	–	12.3	9.4
Mystic River	Echo Spring	1548	0.6–1.3[a]/12.7[c]	956	75.8	1.8
Roaring River/Shrimp Pools	Echo Spring	1371	2.2[c]	441	125.4	16.5
Colossal River	Pike Spring	1116	3.5[b]/3.4[c]	–	63.8	8
Eyeless Fish Trail	Pike Spring	726	1.6[b]/3.3[c]	726	67.8	3.7
Logsdon River/Bridge Ave.	Turnhole	913	2.2[c]	–	232.3	0.3
Logsdon River/Hawkins River	Turnhole	570	6.1[c]	1370	90	3.2
Owl Cave	Turnhole	11	–	2849	0	1
Brown River	Turnhole (Parker Cave)	100	–	–	900	–
Parker River	Turnhole (Parker Cave)	200	–	–	125	–
North Creek	Turnhole (Parker Cave)	150	–	–	1133	–
Sulphur River	Turnhole (Parker Cave)	225	–	–	405	20

[a] Whitman (1989)
[b] Poulson (1992)
[c] Pearson and Jones (1998)
[d] Fowler, unpublished

regional cave aquatic ecosystem. However, their origin and energetic content can be inferred based on the bacterial community found in area cave streams.

DNA analysis of bacterial biofilms grown on artificial substrates in MCNP's cave aquatic habitats (i.e., Owl cave, Hawkins/Logsdon confluence, Charon's Cascade, Mystic River, and Eyeless Fish Trail) suggests a diverse phylogenetic groups of bacterial communities are able to exploit a wide range of environmental conditions due to a wide range of metabolic processes (Fowler et al. 2009*). Proteobacteria, a group that includes both consumers and producers, were the dominant phyla and made up greater than 50% of all bacterial DNA found among all cave stream sites. Alphaproteobacteria, which are known to grow at very low nutrient levels, were the dominant group at most cave stream sites. DNA from gamma- and deltaproteobacteria, groups that include common gut fauna in animals, predators on other bacteria, and contributors to the sulfur cycle as producers of hydrogen sulfide under anaerobic conditions, was also found at most cave stream sites. Intriguingly, DNA from betaproteobacteria, a group that includes chemoautotrophs, was also found at all cave stream sites. The presence of alpha- and betaproteobacteria at most MCNP cave streams sites suggests they do not utilize POM subsidies from the surface as their primary energy source but instead rely on likely energy sources such as dissolved organic matter or chemoautotrophy. Cave stream sites such as Hawkins/Logsdon and Owl Cave, however, appear to be organically enriched due to agricultural input from watersheds

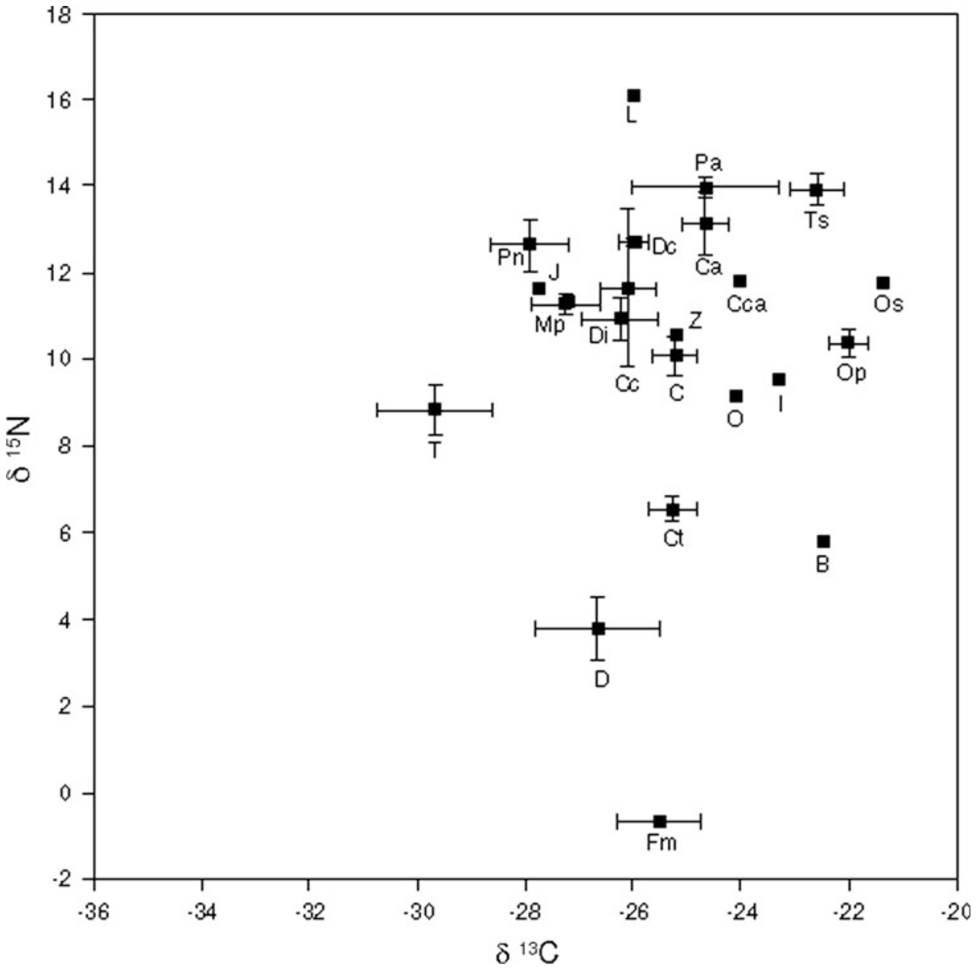

Fig. 14.13 Cave composite graph of temporally and spatially pooled δ^{13}C and δ^{15}N data (Compson 2004). Bacteria (B); *Cambarus tenebrous* (Ct); Chironimidae (C); *Forbesichthys agassizi* (Ca); *Cottus carolinae* (Cc); *Cyprinus carpio* (Cca); detritus (D); Diptera (Di); *Dorosoma cepedianum* (Dc); fungal mycelia (Fm); Isopoda (I); larval fish (L); *Micropterus punctulatus* (Mp); Oligochaeta (O); *Orconectes pellucidis* (Op); Ostracoda (Os); *Pimephales notatus* (Pn); *Pomoxis annularis* (Pa); tadpole (T); *Typhlichthys subterraneus* (Ts); and Zooplankton (Zo). Used with permission

outside the park. Indeed, their data showed total microbial biomass on artificial substrates in MCNP's deep cave aquatic habitats decreased from organically enriched cave streams, with input from watersheds outside MCNP's boundaries, to "pristine" cave streams whose watersheds are entirely within park boundaries: Owl cave ≫ Hawkins/Logsdon > Roaring River ≫ Eyeless Fish Trail > Mystic River. There may also be chemoautotrophic energy inputs provided by sulfur oxidizing bacteria and possibly some energy provided by hydrocarbon oxidizing bacteria. The relative magnitudes of the latter two energy inputs are unknown at this time.[1]

14.4 Chemoautotrophy and Potential Support of Troglobionts via Hydrocarbon Energy Inputs

Cutting across the Central Kentucky Karst is a warp in the bedrock along an east–west band where sulfurous brine rises under artesian conditions. Parker Cave is developed within this structural feature and has three streams that receive sulfurous brine (Fig. 14.2). Sulfur oxidizing bacteria use hydrogen sulfide to make organic carbon through a process called chemosynthesis. Although chemosynthesis is analogous to photosynthesis, the difference is that it occurs regardless of light level or season. Of the three streams with sulfides in Parker Cave, Sulphur River is the most studied (Angert et al. 1998; Olson and Thompson 1988; Roy 1988; Thompson and Olson 1988). These organic-rich cave streams drain into Mammoth Cave and so provide biomass that would not otherwise exist. Other sites along the warp in the bedrock may also provide energy to Mammoth Cave, but they are not yet documented. Indirect methods of investigation further downstream may help gauge the relative contributions to cave streams from photosynthetic versus

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[1] An unpublished poster titled "Concentration and Diversity of Bacteria in Clastic Sediments and Limestone Biofilms of Mammoth Cave, Kentucky" by Rick Fowler, Rick Olson, Hazel Barton, and Shivendra Sahi, a progress report to the National Cave and Karst Research Institute in Carlsbad, NM. The poster is stored in the Mammoth Cave National Park Curatorial Facility, accession number 818.

chemosynthetic sources. For more discussion on this subject see Chap. 16.

Hydrogen sulfide-laden fresh water is common regionally due to sulfate minerals within the St. Louis Limestone. Unlike the brines rising in Parker Cave, these sulfides are shallow and several streams in Mammoth Cave are vertically less than 100 feet and maybe as little as 50 feet (30.5 − 15 m) above this sulfide rich zone. To migrate up, all they need is a fracture or a fault, and there are plenty of these. Artesian conditions in this sulfate zone are known to occur, and it makes perfect sense due to the regional northwest dip of the bedrock housing Mammoth Cave. These hydrogeological conditions and their potential biological significance to Mammoth Cave ecosystems are just now being considered (Olson, in press).

A sulfur spring was reported within Mammoth Cave in the mid-1800s (Bullitt 1845), and Hebes Spring, reported by Hovey (1912), is likely the same feature. These seeps, located in Marianne's Pass, contain low concentrations of hydrogen sulfide, which support bacterial mats typical of sulfur oxidizing bacteria. To date no similar seeps have been found in the cave, but Cave Research Foundation explorers have not been trained to recognize them, and there are thousands of tiny passages where similar seeps might exist. Such training for cavers has been identified as a top priority by microbiologists (Barton 2006). Both hydrogen sulfide and hydrocarbons are very abundant in the Mammoth Cave region which is one hypothesis helping explain the high diversity of troglobionts in the region (Olson 2013). This could represent another paradigm shift regarding Mammoth Cave in the views of biospeleologists. For details on biodiversity in Mammoth Cave see Chaps. 1 and 15. Hydrocarbon odors are associated with the sulfurous seeps in Mariannes Pass, and such sources of organic carbon could also be an auxiliary source of energy to Mammoth Cave ecosystems (Olson, in press) as it is in the Edwards Aquifer. For more discussion of hydrocarbons in Mammoth Cave see Chap. 10 (Meteorology).

14.4.1 A Case Study of Recovery from Severe Cave Stream Pollution

The strongest data available regarding the ecological effects of nonpoint and chronic point source pollution on a cave aquatic community in the Mammoth Cave region, including its post-mitigation succession and recovery, are available from long-term monitoring data in Hidden River Cave (Jones and Pearson 1997; Lewis 1995). Located beneath Horse Cave, KY Hidden River Cave was a tourist attraction and water source for the town in the early twentieth century until groundwater pollution ended the latter practice. In 1944, a local creamery began discharging its waste into the cave and both Horse Cave and Cave City began discharging their sewage effluent into the cave; the former town's effluent containing a mixture of domestic and industrial sewage (Lewis 1995). In the early 1980s, Lewis (1982) began monitoring the cave's aquatic community finding large numbers of aquatic organisms indicative of high nutrient loading: sewage fungus, sewage bacteria, and tubificid worms. Subsequent surveys every few months following the dedication of a new sewage regional treatment facility in the winter of 1989 showed little change in the community though, interestingly, Lewis (1995) observed a single individual of the surface crayfish *C. tenebrosus* and the stygobiotic isopod *C. bicrenata* (Table 14.3). In late 1991, *C. tenebrosus* were observed in high abundance, a condition which continued for the next several years, indicating a cave stream habitat still enriched enough to support large numbers of surface crayfish. In March 1993, the first stygobiotic cavefish (i.e., *T. subterraneus*) and several cave salamanders (*Eurycea lucifuga*), indicating further recovery of the cave aquatic community, were observed. In October 1993, Lewis finally observed *O. pellucidus* and *T. subterraneus* in abundances greater than surface stream organisms. Nearly a decade later, Lewis et al. (2015) observed diversity in Hidden River's Cave's stream community remained relatively low (Table 14.3). Jones and Pearson (1997) speculated the high abundance of *T. subterraneus* they found was due to a reproductive event in 1993, presumably due to high numbers of observed juveniles, where slight decreases in later years reflected local population "adjustments". Their final observations in October 1995, which included the amphipod *C. barri*, suggest the cave aquatic community was near full recovery; though a few typical accidentals (i.e., a green frog *R. clamitans*, a surface fish, and a salamander larva) were also present (Table 14.3). The utility of long-term monitoring data, collected by trained professionals via systematic biological surveys, to resource management at MCNP cannot be overstated.

14.5 Future Directions in Long-Term Monitoring

The overall purpose of natural resources monitoring in parks is to provide scientifically sound information on the current status and long-term trends in the composition, structure, and function of park ecosystems to park resource managers. Use of monitoring information increases confidence in managers' decisions, improves their ability to manage park resources, and enables them to confront and mitigate threats to the park and operate more effectively in legal and political arenas. Critical to resource managers is information on whether the true absence of a species of concern from specific habitats indicates the habitat is simply unoccupied, marginal, or

Table 14.3 Successional recovery of Hidden River Cave stream community after sewage diversion/treatment

Species	1982 (November)	1989	1990 (March)	1990 (Oct)	1990 (Dec)	1991 (Oct)	1993 (March)	1993 (July)	1993 (Oct)	1994 (Aug)	1994 (Oct)	1995 (Oct)	2013 (June)	2013 (Sept)	2013 (Nov)	2014 (Jan)	2014 (June)	2014 (July)	2014 (Aug)	2014 (Sept)
Tubificid Worms	X	X	X		X															
Sewage Fungus	X	X																		
Sewage Bacteria	X	X	X	X	X															
Isopod				1			1	21	18	62	3	1		14			51	8	17	
Amphipod								2	3	3	0	1							1	
C. tenebrosus			1	1		45	29		33	39	14	3	1	2	1		1		1	
O. pellucidus								12	70	109	7	122	1	21	17	8	22	1	15	52
E. lucifuga							3													
T. subterraneus							1	5	29	22	1	19		2						2
Surface Fish												1								
Salamander								1	17	2		1								
Frog									1			1								

degraded (Peterman et al. 2013; Peterson et al. 2013). For example, one of the arguments made by Lisowski and Poulson (1979) for removing the recently failed Lock and Dam #6, just downstream of the Green River segment flowing through MACA, was that with the dam in place-specific cave aquatic habitats saw increased siltation, decreased habitat heterogeneity, and reduced abundance of the federally endangered Kentucky cave shrimp *P. ganteri*. However, the failure to detect a species is not necessarily an indication it is absent from the community. Indeed, a monitoring method that fails to distinguish between whether a species is present and undetected or absent severely limits its utility to resource managers. Because these two states are not distinguishable, the likelihood of a species being associated with particular habitats (e.g., ecotonal cave spring habitat), even when it is not detected, must be estimated.

Future monitoring will utilize rigorous methods to determine cave aquatic organisms' habitat associations and their area of occurrence. State-of-the-art statistical modeling will be used to analyze counts of organisms and data on their presence/absence and so provide resource managers with valuable information regarding whether the absence of a target species from specific habitats indicates the habitat is simply unoccupied, marginal, or impacted (Peterman et al. 2013). Implementing a rigorous monitoring protocol for cave aquatic biota and their habitat covariates provides an excellent opportunity to gather baseline data on current habitat associations among cave aquatic biota before these changes occur as well as test prior predictions based on past research.

References

Angert ER, Northup DE, Reysenbach AL, Peek AS, Boebel BM, Pace NR (1998) Molecular phylogenetic analysis of a bacterial community in Sulphur River, Parker Cave, Kentucky. Am Miner 83:1583–1592

Barr TCJ (1967) Ecological studies in the Mammoth Cave System of Kentucky. I. The biota. Int J Speleol 3:147–203

Barr TCJ, Kuehne RJ (1971) Ecological studies in the Mammoth Cave system of Kentucky. II. The ecosystem. An de Spéléologie 26: 48–96

Barton HA (2006) Introduction to cave microbiology: a review for the non-specialist. J Cave Karst Stud 68:43–54

Bullitt A (1845) Rambles in the Mammoth Cave during the year 1844 by a visitor. Morton and Griswold, Louisville, Kentucky, p 88

Christman MC, Doctor DH, Niemiller ML, Weary DJ, Young JA, Zigler KS, Culver DC (2016) Predicting the occurrence of cave-inhabiting fauna based on features of the earth surface environment. PLoS ONE 11:e0160408

Compson ZG (2004) An isotopic examination of cave, spring and epigean trophic structures in Mammoth Cave National Park. M.S. Western Kentucky University

Cooper JE, Cooper MR (2010) Observations on the biology of the endangered stygobiotic shrimp *Palaemonias alabamae*, with notes on *P. ganteri* (Decapoda: Atyidae). Subterranean Biol 8:9–20

Culver DC, Holsinger JR, Christman MC, Pipan T (2010) Morphological differences among eyeless amphipods in the genus Stygobromus dwelling in different subterranean habitats. J Crustac Biol 30:68–74

Culver DC, Pipan T (2009) The biology of caves and other subterranean habitats. Oxford University Press, New York

Gittleson S, Hoover R (1970) Protozoa of underground waters in caves. Ann Speleol 25:91–106

Hobbs HH III, Daniel MA (1977) A review of the troglobitic decapod crustaceans of the Americas. Smithson Contrib Zool 244:1–183

Hovey H (1912) Mammoth Cave of Kentucky. John P. Morton & Company, Louisville, Kentuck, p 87

Hubricht L (1943) Studies in the Nearctic Freshwater Amphipoda, III. Am Midl Nat 29:683–712

Jones TG, Pearson WD (1997) The recovery of the aquatic biological community in Hidden River Cave, Horse Cave, Kentucky. In: Sixth annual Mammoth Cave National Park science conference. National Park Service, Mammoth Cave, Kentucky, p 231

Kenk R (1977) Freshwater Triclads (Turbellaria) of North America, IX: the genus *Sphalloplana*. Smithson Contrib Zool 246:38

Lewis JJ (1988) The systematics, zoogeography and life history of the troglobitic isopods of the Interior Plateaus of the eastern United States. University of Louisville, Kentucky

Lewis JJ (1995) The devastation and recovery of caves and karst affected by industrialization. In: 1995 National Cave management symposium. National Cave and Karst management symposia. Spring Mill State Park, Indiana, pp 214–227

Lewis JJ, Lewis TM, Eckstein J (1982) A biological reconnaissance of a polluted cave stream: the hidden river groundwater basin. Cave Research Foundation 1982 Annual Report: 9–10

Lewis JJ, Lewis S, Nims P (2015) Observations on the ecosystem of hidden river cave bioinventory: community census and water quality analysis. Kentucky Heritage Land Conservation Fund

Lisowski EA, Poulson TL (1979) Impacts of Lock and Dam Six on base level ecosystems in Mammoth Cave. Cave Research Foundation 1979 Annual Report: 48–54

Niemiller M, Fitzpatrick B (2012). Status and life history of the Amblyopsid Cavefishes in Kentucky. Kentucky Department of Fish and Wildlife Resources

Niemiller M, Poulson TL (2010) Subterranean fishes of North America: Amblyopsidae. In: Trajano E, Bichuette M, Kapoor B (eds) Biology of subterranean fishes. Science Publishers, Enfield, pp 169–282

Olson R (2013) Potential effects of hydrogen sulfide and hydrocarbon seeps on Mammoth Cave ecosystems. In: Mammoth Cave National Park's 10th research symposium. Mammoth Cave, KY, pp 25–30

Olson R (in press) Sulfides in the Mammoth Cave area. In: Klimchouk A, Palmer AN, Audra P, DeWaele J, Auler A (eds) Hypogene Karst areas and caves of the world. Springer International Publishing, Cham, Switzerland

Olson R, Thompson B (1988) Scanning electron microscopy and energy dispersive X-ray analysis of artificial and natural substrates from the Phantom flowstone of Sulphur River in Parker Cave, Kentucky. Bull Natl Speleol Soc 50:47

Pearson WD, Jones TG (1998) A final report based on faunal inventory of subterranean streams and development of a cave aquatic biological monitoring program using a modified index of biological integrity. National Park Service, Mammoth Cave National Park, p. 139

Peterman WE, Crawford JA, Kuhns AR (2013) Using species distribution and occupancy modeling to guide survey efforts and assess species status. J Nat Conserv 21:114–121

Peterson EE, Ver Hoef JM, Isaak DJ, Falke JA, Fortin M-J, Jordan CE, McNyset K, Monestiez P, Ruesch AS, Sengupta A, Som N, Steel EA, Theobald DN, Torgersen CE, Wenger SJ (2013)

Modelling dendritic ecological networks in space: an integrated network perspective. Ecol Lett 16:707–719

Pipan T, Christman MC, Culver DC (2006) Dynamics of epikarst communities: microgeographic pattern and environmental determinants of epikarst copepods in Organ Cave, West Virginia. Am Midl Nat 156:75–87

Pipan T, Culver DC (2013) Forty years of epikarst: what biology have we learned? Int J Speleol 42:215–223

Pipan T, Holt N, Culver DC (2010) How to protect a diverse, poorly known, inaccessible fauna: identification and protection of source and sink habitats in the epikarst. Aquat Conser Mar Freshw Ecosyst 20:748–755

Poly WJ, Boucher CE (1996) Nontroglobitic fishes in caves: their abnormalities, ecological classification and importance. Am Midl Nat 136:187–198

Poulson TL (1992) The Mammoth cave ecosystem. In: Camacho A (ed) The natural history of biospeleology. Museo Nacional de Ciencias Naturales, Madrid, pp 569–611

Roy W (1988) Preliminary assessment of the solution equilibria of Sulphur River in Parker Cave, Kentucky. Bull Nat Speleol Soc 50:37–41

Ruhl M (2005) Flow reversal events increase the abundance of nontroglobitic fish in the subterranean rivers of Mammoth Cave National Park. Western Kentucky University, Kentucky

Simon KS, Benfield EF (2001) Leaf and wood breakdown in cave streams. North Am Benthol Soc 20:550–563

Simon KS, Benfield EF, Macko SA (2003) Food web structure and the role of epilithic biofilms in cave streams. Ecology 84:2395–2406

Simon KS, Pipan T, Culver DC (2007) A conceptual model of the flow and distribution of organic carbon in caves. J Cave Karst Stud 69:279–284

Taylor MS, Blechle BE, Pobst BS (2010) Morphological divergence between cave and surface populations of the digger crayfish, *Fallicambarus fodiens* (Cottle, 1863) (Decapoda, Cambaridae). Crustaceana 83:1303–1313

Thompson B, Olson R (1988) A preliminary survey of the protozoa and bacteria from Sulphur River in Parker Cave, Kentucky. Bull Nat Speleol Soc 50:42

Trimboli S, Toomey III RS, Weber K, Ryan S (2016) An overview of the reverse flow patterns of River Styx in Mammoth Cave, Kentucky: 2009–2012. In: Mammoth Cave National Park's 11th research symposium: celebrating diversity of research in the Mammoth Cave Region. Western Kentucky University, Mammoth Cave National Park, pp 128–129

Tumlinson R, Cline GR (2002) Food habits of the Banded Sculpin (*Cottus carolinae*) in Oklahoma with reference to predation on the Oklahoma salamander (*Eurycea tynerensis*). Proc Okla Acad Sci 82:111–113

United States Fish and Wildlife Service (1988) Kentucky cave shrimp recovery plan. United State Fish Wildlife Service, Atlanta

Whitman RL (1989) Meiofaunal sampling at Mammoth Cave National Park, draft report. National Park Service, Indiana Dunes National Lakeshore

Zhang J, Holsinger JR (2003) Systematics of the freshwater amphipod genus Crangonyx (Crangonyctidae) in North America. Virginia Mus Nat Hist Mem 6:274

Ziemba RE, Simpson A, Hopper R, Cooper RL (2003) A comparison of antennule structure in a surface- and a cave-dwelling crayfish, genus Orconectes (Decapoda, Astacidae). Crustaceana 76:859–869